J. Helminthol. Soc. Wash.
61(1), 1994, pp. 67–72

Parasites of Alewives, *Alosa pseudoharengus,* from the Great Lakes

PATRICK M. MUZZALL
Department of Zoology, Natural Science Building, Michigan State University,
East Lansing, Michigan 48824

ABSTRACT: A total of 302 alewives, *Alosa pseudoharengus* (Clupeidae), were collected from 2 locations in Lake Michigan and from Saginaw Bay, Lake Huron, between May 1990 and July 1992 and examined for parasites. Ten parasite species (2 Trematoda, 4 Cestoda, 1 Nematoda, 1 Acanthocephala, 1 Copepoda, and 1 Protozoa) infected alewives from Lake Michigan, with *Echinorhynchus salmonis* Müller, 1784, being most common. *Diplostomum* sp., *Contracaecum* sp., and *Ergasilus luciopercarum* Henderson, 1927, infrequently infected alewives from Saginaw Bay. Alewives from Ludington, Michigan, had the highest mean parasite species richness (0.7229). A summary and comparison of the parasites found in alewives from the Great Lakes are presented with 22 parasite species reported. This information revealed that the alewife is an important intermediate and transport host for helminths that mature in piscivorous fishes and birds in the Great Lakes area.

KEY WORDS: alewife, *Alosa pseudoharengus,* Clupeidae, parasites, survey, Michigan, Great Lakes.

The alewife, *Alosa pseudoharengus* (Wilson), is an anadromous fish species of eastern North America (Scott and Crossman, 1973). Its origin in the Great Lakes has not been established with certainty (R. R. Miller, 1957). The alewife was first reported in Lake Huron in 1933 and in Lake Michigan in 1949, and since then it has become well established in many parts of these lakes. The importance of the alewife as a food item for salmonids (Jude et al., 1987; M. A. Miller and Holey, 1992) and piscivorous birds (Ludwig, 1966; Fox et al., 1990) in the Great Lakes is well known.

The objectives of the present study were (a) to provide information on the occurrence and abundance of parasites in alewives from 2 locations in Lake Michigan and from the western portion of Saginaw Bay, Lake Huron; (b) to summarize and compare the known information about parasites infecting this important forage species in the Great Lakes; and (c) to examine the role of alewives as intermediate and transport hosts for parasites that mature in piscivorous fishes and birds in the Great Lakes area.

Materials and Methods

Alewives were collected by beach seine and trawl from 2 locations in Lake Michigan and from the western portion of Saginaw Bay, Lake Huron. Fish data are given below with information on location; month and year of collection; number of fish examined; total length, with range in millimeters (followed by mean ± SD); and 95% confidence intervals.

1. Southern Lake Michigan, Michigan City, Indiana; August 1991; $n = 75$; 101–212 (151 ± 29.1); 144.1–157.5.
2. Eastern Lake Michigan, Ludington, Michigan; May–August 1990, April–June 1991; $n = 166$; 102–239 (160 ± 28.6); 155.8–164.6.
3. Western portion of Saginaw Bay, Lake Huron, Michigan; May–July 1992; $n = 61$; 62–203 (141 ± 35.1); 132.1–150.1.

Ludington, Michigan, is approximately 247 km north of Michigan City, Indiana. Alewives were frozen in the field and measured and sexed at necropsy. The skin, fins, gills, eyes, kidney, gonads, spleen, liver, gall bladder, mesenteries, esophagus, gastrointestinal tract, heart, and the left or right side of the musculature were examined. Parasites were collected and processed using routine procedures. Prevalence is the percentage of fish infected, and mean intensity is the mean number of worms of a species per infected fish. Voucher specimens have been deposited in the U.S. National Parasite Collection, Beltsville, Maryland 20705: *Diplostomum* sp. (83226), *Tetracotyle* sp. (83227), *Cyathocephalus truncatus* (83228), *Diphyllobothrium* sp. (83229), *Eubothrium salvelini* (83230), *Proteocephalus* sp. (83231), *Haplonema hamulatum* (83233), and *Echinorhynchus salmonis* (83232). Specimens of *Ergasilus luciopercarum* are in the collection of L. Roberts. Specimens of other helminth species were not retained by the author and therefore were not deposited.

Information on the parasites of alewives was obtained from examining published studies performed in the Great Lakes. Species richness refers to the number of parasite species infecting alewives from each Great Lake. The Jaccard coefficient of community similarity was calculated as

$$CC_j = C/(S_1 + S_2 - C),$$

where S_1 and S_2 are the number of parasite species in communities 1 and 2, respectively, and C is the number of species common to both communities (Brower and Zar, 1984). For calculations of the Jaccard coefficient of community similarity and species richness, *Diplostomum* (present study) and *Diplostomulum* in other studies were considered to be a single genus.

Results

Thirty (40%) alewives from Michigan City, Indiana, 91 (55%) from Ludington, Michigan, and 7 (11%) from Saginaw Bay, Michigan, were infected with 1 or more parasites. A total of 10 parasite species (4 from Michigan City and 9 from Ludington) infected alewives from both locations in Lake Michigan (Table 1). *Echinorhynchus salmonis* had the highest prevalence and mean intensity at each location. Correlation coefficients between *E. salmonis* intensity and length of infected alewife from Michigan City and Ludington were 0.172 ($P > 0.05$) and 0.592 ($P < 0.01$), respectively. Of the helminth species found, only *Cyathocephalus truncatus* (Pallus, 1781) and *E. salmonis* were gravid. *Diplostomum* sp. was more common in alewives from Michigan City than from Ludington, whereas cestodes were more common in alewives from Ludington than from Michigan City. Three parasite species (*Diplostomum* sp., *Contracaecum* sp., and *Ergasilus luciopercarum*) infrequently infected alewives from Saginaw Bay. There were no significant differences in prevalence (chi-square analysis, $P > 0.05$) and intensity (Student's t-test, $P > 0.05$) of parasitism between female and male alewives at each location. The alewife is a new host record for *Haplonema hamulatum* Moulton, 1931, and *E. luciopercarum*.

Jaccard's coefficients of similarity for the parasite faunas of alewives between locations are 0.30 for Michigan City–Ludington, 0.40 for Michigan City–Saginaw Bay, and 0.09 for Ludington–Saginaw Bay. When the data for uninfected and infected fish were combined, mean parasite species richness ± SD, range, and 95% confidence intervals in alewives from Michigan City (0.5333 ± 0.6830, 0–2, 0.3670–0.6997), from Ludington (0.7229 ± 0.7991, 0–4, 0.6016–0.8441), and from Saginaw Bay (0.1148 ± 0.3214, 0–1, 0.0324–0.1971) were significantly different (analysis of variance, $F = 16.7$, $P < 0.001$). However, when data from infected fish only were used in the analyses, mean parasite species richness ± SD, range, and 95% confidence intervals in alewives from Michigan City (1.3333 ± 0.4795, 1–2, 1.1543–1.5124), from Ludington (1.3187 ± 0.5940, 1–4, 1.1949–1.4424) and from Saginaw Bay ($\bar{x} = 1$, range = 1) were not significantly different (analysis of variance, $F = 1.13$, $P > 0.05$).

Discussion

Echinorhynchus salmonis was the most common parasite species found in alewives from Lake Michigan in the present study. Alewives in this lake feed on the amphipod, *Pontoporeia affinis,* which serves as an intermediate host for this parasite (Amin, 1978). Morsell and Norden (1968) reported that as alewives in western Lake Michigan increased in length a greater proportion of *P. affinis* was found in their diet. This could explain the significant relationship between *E. salmonis* intensity and length of infected alewives from Ludington, Michigan. Webb and McComish (1974) found that the largest percentage of volume and percent frequency of occurrence of *P. affinis* in alewives from southern Lake Michigan occurred in August 1972; however, it was of negligible importance in their diet in 1971. Rhodes and McComish (1975) reported that alewives consumed the largest volume of *P. affinis* in October in southern Lake Michigan.

Amin and Burrows (1977) found *E. salmonis* infecting alewives in western Lake Michigan. A mean intensity of 1.9 *E. salmonis* per infected fish was calculated using their data in Table 1. This value and prevalence are low compared to the infection values of *E. salmonis* in the present study. Fish length and time of collection do not appear to play major roles in these infection differences, because examined fish had similar lengths and were collected during similar months. Possible explanations for these infection differences may involve the availability of the amphipod intermediate host and its importance in the diet of alewives from 1 year to the next or *E. salmonis* may be more common in 1 location than in another.

Muzzall (1989) hypothesized that the alewife serves as an important transport host for *E. salmonis* to salmonids in eastern Lake Michigan. Hnath (1969) experimentally demonstrated the transfer of *E. salmonis* between coho salmon, *Oncorhynchus kisutch,* and brook trout, *Salvelinus fontinalis,* from Lake Michigan. Jude et al. (1987) reported that the alewife made up 78% of the identifiable prey species eaten by salmonids in Lake Michigan. The high infection values of *E. salmonis* in alewives in the present study supports this suggestion that alewives serve as important transport hosts for *E. salmonis* to salmonids. Seng (1975) estimated that approximately one-eighth of *E. salmonis* flows through transport hosts in the ecosystem of Cold Lake, Alberta. Furthermore, it is known that as salmonids become older (larger) they ingest a larger proportion of alewives (Muzzall, 1989). Amin and Burrows (1977) suggested that other species of

Table 1. **Prevalence (P), mean intensity (MI), and maximum number of parasites (max.) found in *Alosa pseudoharengus* from Lake Michigan (Michigan City, Indiana, and Ludington, Michigan) and Saginaw Bay, Lake Huron, 1990-1992.***

Parasite	Michigan City (n = 75)†		Ludington (n = 166)		Saginaw Bay (n = 61)		Site
	P	MI ± 1 SD (max.)	P	MI ± 1 SD (max.)	P	MI ± 1 SD (max.)	
Digenea							
Diplostomum sp.‡	21	1.6 ± 1.0 (4)	0.6	1	3	1	Lens
Tetracotyle sp.‡	—	—	1	1	—	—	Encysted in mesenteries
Cestoda							
Cyathocephalus truncatus	—	—	12	1.6 ± 0.9 (4)	—	—	Pyloric ceca
Diphyllobothrium sp.‡	—	—	0.6	1	—	—	Encysted around pyloric cecum
Eubothrium salvelini§	—	—	8	2.0 ± 1.5 (5)	—	—	Anterior intestine, pyloric ceca
Proteocephalus sp.§	1	1	1.8	1	—	—	Anterior intestine
Nematoda							
Contracaecum sp.‡	—	—	—	—	5	3.7 ± 1.5 (5)	Encysted in mesenteries
Haplonema hamulatum§	—	—	1	1	—	—	Small intestine
Acanthocephala							
Echinorhynchus salmonis	29	4.0 ± 3.4 (13)	48	8.4 ± 11.3 (72)	—	—	Intestine
Copepoda							
Ergasilus luciopercarum	1	1	—	—	3	1	Gills
Protozoans							
Trichodina sp.	—	—	0.6	—	—	—	Gills

* Unless otherwise indicated, parasites were gravid.
† Number of fish examined.
‡ Metacercariae or larvae.
§ Immature parasites.

Table 2. Parasites reported from *Alosa pseudoharengus* in the Great Lakes.

Parasite	Lake Michigan ($n = 241$)*	Lake Superior ($n = 12$)	Lake Huron ($n = 297$)	Lake Erie ($n = 14$)	Lake Ontario ($n = 61$)
Monogenea					
Octomacrum sp.	—	—	—	10	—
Digenea					
Diplostomum flexicaudum	—	—	7	—	—
Diplostomum spathaceum	—	5	6, 8	—	12
Diplostomum sp.	1, 2	—	9	10	—
Posthodiplostomum minimum	—	—	—	—	12
Tetracotyle intermedia	—	—	6	—	—
Tetracotyle sp.	2	—	8	—	—
Metacercariae	—	—	—	10	—
Cestoda					
Cyathocephalus truncatus	2	—	—	—	—
Diphyllobothrium sp.	2	—	—	—	—
Eubothrium salvelini	2	—	—	—	—
Proteocephalus sp.	1, 2	—	—	—	—
Nematoda					
Camallanus oxycephalus	—	—	—	11	—
Capillaria sp.	—	—	—	10	—
Contracaecum sp.	—	—	9	—	—
Haplonema hamulatum	2	—	—	—	—
Acanthocephala					
Acanthocephalus dirus	3	5	6, 7, 8	—	12
Echinorhynchus salmonis	1, 2, 4	—	6, 7	—	—
Copepoda					
Ergasilus luciopercarum	1	—	9	—	—
Fungi					
Saprolegnia sp.	—	5	6, 7, 8	—	12
Protozoa					
Trichodina sp.	2	—	—	—	—
Acarina					
Hydrachna sp.	—	—	6	—	—

* Total number of fish examined. Entries are abbreviations for published investigations on the parasites of alewives from the Great Lakes. 1 = present study, Michigan City, Indiana; 2 = present study, Ludington, Michigan; 3 = Amin (1977); 4 = Amin and Burrows (1977); 5 = Dechtiar and Lawrie (1988); 6 = Collins and Dechtiar (1974); 7 = Dechtiar and Berst (1978); 8 = Dechtiar et al. (1988); 9 = present study, Saginaw Bay, Michigan; 10 = Bangham (1972); 11 = Stromberg and Crites (1975); 12 = Dechtiar and Christie (1988).

forage fish in Lake Michigan serve as transport hosts for *E. salmonis*.

This is the first published study to summarize the parasites of a fish species in the Great Lakes with a total of 22 parasite species being reported from the alewife (Table 2). Taxonomically, larval digenean species are most common followed by cestode and nematode species. No parasite species has been reported from alewives in all the Great Lakes. *Diplostomum* is the only genus found in alewives from all the Great Lakes. Cestodes were reported from alewives only from Lake Michigan. *Acanthocephalus dirus* has been found in alewives from 4 Great Lakes. Although *E. salmonis* infect fishes from Lake Huron, it was not found in alewives from Saginaw Bay. None of the parasite species infecting alewives in the Great Lakes is specific to this fish species.

Mean parasite species richness was significantly higher in alewives from Ludington than from the other locations because more parasite species were found and the high prevalence of *E. salmonis*. Parasite species richness (in parentheses) in alewives from each lake are Lake Mich-

Table 3. Jaccard's index of community similarity based on presence of parasite species reported from *Alosa pseudoharengus* in each lake.*

Lake†	1	2	3	4	5
1	1.0	0.08	0.29	0.07	0.07
2		1.0	0.27	0.00	0.75
3			1.0	0.07	0.15
4				1.0	0.00
5					1.0

* See Table 2 for the parasite species used in these calculations and specific investigations.

† 1 = Lake Michigan, 2 = Lake Superior, 3 = Lake Huron, 4 = Lake Erie, 5 = Lake Ontario.

igan (11), Lake Superior (3), Lake Huron (11), Lake Erie (5), and Lake Ontario (4). Species richness is highest in Lake Michigan and Lake Huron, where the largest numbers of alewives were examined. Jaccard's coefficients of similarity for the parasite faunas in alewives between the Great Lakes do not follow a specific pattern (Table 3). Alewives from Lake Erie had the lowest coefficients (≤0.07), indicating that they shared the fewest parasite species with alewives from the other Great Lakes. Alewives from Lake Superior and Lake Ontario had the highest coefficient (0.75), indicating that they shared the most parasite species of those species found in alewives from each lake.

Several hypotheses have been proposed and discussed by Wisniewski (1958), Chubb (1963, 1964, 1970), Esch (1971), Halvorsen (1971), Kennedy (1978), Holmes and Price (1986), and Marcogliese and Cone (1991) to explain the patterns of distribution and abundance of metazoan parasites in freshwater fishes. The present study is the first to investigate the distribution of parasites in 1 fish species in the Great Lakes. None of these hypotheses, however, explains the distribution and number of helminth species in alewives from the Great Lakes. An explanation is confounded by the small number of alewives examined from Lake Superior and Lake Erie. It is believed more parasite species will be found when more alewives are examined from these 2 lakes.

Eight (7 larval digenean species and *Diphyllobothrium* sp.) of the 18 helminth species reported from alewives in the Great Lakes (Table 2) are allogenic, maturing in piscivorous birds. Both Ludwig (1966) and Fox et al. (1990) have reported that the alewife and rainbow smelt, *Osmerus mordax,* accounted for at least 80% of the fish eaten by herring gulls, *Larus argentatus,* in the Great Lakes. *Eubothrium salvelini* (Schrank, 1790), *Proteocephalus* sp., *Capillaria* sp., *Contracaecum* sp., and *Haplonema hamulatum,* listed in Table 2, mature in other fish species and not in the alewife. It is believed that alewives serve as transport hosts for these helminth species and *E. salmonis.* Therefore, it is hypothesized that the dominance of allogenic helminth species in alewives and the occurrence of helminths in alewives that mature in other fish species is attributable to the position of alewives in the food web as planktivores and macroinvertivores that are prey species for piscivorous fishes and birds in the Great Lakes area.

Acknowledgments

I thank Dan Brazo, Indiana Department of Natural Resources, Michigan City, Indiana, and Tom McComish, Ball State University, Muncie, Indiana; Rob Elliott and Doug Peterson, Michigan State University, East Lansing, Michigan; and Bob Haas, Jack Hodge, and Larry Shubel, Michigan Department of Natural Resources, Mount Clemens, Michigan, for providing the alewives; and Larry Roberts for confirming my identification of *Ergasilus luciopercarum.*

Literature Cited

Amin, O. M. 1977. Helminth parasites of some southwestern Lake Michigan fishes. Proceedings of the Helminthological Society of Washington 44: 210–217.

———. 1978. On the crustacean hosts of larval acanthocephalan and cestode parasites in southwestern Lake Michigan. Journal of Parasitology 64:842–845.

———, **and J. M. Burrows.** 1977. Host and seasonal associations of *Echinorhynchus salmonis* (Acanthocephala: Echinorhynchidae) in Lake Michigan fishes. Journal of the Fisheries Research Board of Canada 34:325–331.

Bangham, R. V. 1972. A resurvey of the fish parasites of western Lake Erie. Bulletin of the Ohio Biological Survey 4:1–23.

Brower, J. E., and J. H. Zar. 1984. Field and Laboratory Methods for General Ecology, 2nd ed. William C. Brown Publishers, Dubuque, Iowa.

Chubb, J. C. 1963. On the characterization of the parasite fauna of the fish of Llyn Tegid. Proceedings of the Zoological Society of London 141:609–621.

———. 1964. A preliminary comparison of the specific composition of the parasite fauna of the fish of Llyn Padarn, Caenarvonshire, an oligotrophic lake, and Llyn Tegid (Bala Lake), Merionetshire, a late oligotrophic or early [*sic*] mesotrophic lake. Wiadomosci Parazytologiczne 10:499–516.

———. 1970. The parasite fauna of British fresh-

water fish. Symposia of the British Society for Parasitology 8:119–144.

Collins, J. J., and A. O. Dechtiar. 1974. Parasite fauna of kokanee salmon (*Oncorhynchus nerka*) introduced into Lake Huron. Journal of the Fisheries Research Board of Canada 31:1818–1821.

Dechtiar, A. O., and A. H. Berst. 1978. Parasite fauna of splake (*Salvelinus fontinalis* × *S. namaycush*). Proceedings of the Helminthological Society of Washington 45:249–254.

———, **and W. J. Christie.** 1988. Survey of the parasite fauna of Lake Ontario fishes, 1961 to 1971. Great Lakes Fisheries Commission, Technical Report 51:66–106.

———, **J. J. Collins, and J. A. Reckahn.** 1988. Survey of the parasite fauna of Lake Huron fishes, 1967 to 1971. Great Lakes Fisheries Commission, Technical Report 51:19–48.

———, **and A. H. Lawrie.** 1988. Survey of the parasite fauna of Lake Superior fishes, 1969 to 1975. Great Lakes Fisheries Commission, Technical Report 51:1–18.

Esch, G. W. 1971. Impact of ecological succession on the parasite fauna in centrarchids from oligotrophic and eutrophic ecosystems. American Midland Naturalist 86:160–168.

Fox, G. A., L. J. Allan, D. V. Weseloh, and P. Mineau. 1990. The diet of herring gulls during the nesting period in Canadian waters of the Great Lakes. Canadian Journal of Zoology 68:1075–1085.

Halvorsen, O. 1971. Studies of the helminth fauna of Norway. XVIII. On the composition of the parasite fauna of coarse fish in the River Glomma, south-eastern Norway. Norwegian Journal of Zoology 19:181–192.

Hnath, J. G. 1969. Transfer of an adult acanthocephalan from one fish to another. Transactions of the American Fisheries Society 98:332.

Holmes, J. C., and P. W. Price. 1986. Communities of parasites. Pages 187–213 *in* J. Kikkawa and D. J. Anderson, eds. Community Ecology: Pattern and Process. Blackwell Scientific Publication, Oxford.

Jude, D. J., F. J. Tesar, S. J. DeBoe, and T. J. Miller. 1987. Diet and selection of major prey species by Lake Michigan salmonids, 1973–1982. Transactions of the American Fisheries Society 116:677–691.

Kennedy, C. R. 1978. An analysis of the metazoan parasitocoenoses of brown trout *Salmo trutta* from British Lakes. Journal of Fish Biology 13:255–263.

Ludwig, J. P. 1966. Herring and ring-billed gull populations of the Great Lakes, 1960–1965. Publication No. 15, Great Lakes Research Division, University of Michigan, Ann Arbor. Pages 80–89.

Marcogliese, D. J., and D. K. Cone. 1991. Importance of lake characteristics in structuring parasite communities of salmonids from insular Newfoundland. Canadian Journal of Zoology 69:2962–2967.

Miller, M. A., and M. E. Holey. 1992. Diets of lake trout inhabiting nearshore and offshore Lake Michigan environments. Journal of Great Lakes Research 18:51–60.

Miller, R. R. 1957. Origin and dispersal of the alewife, *Alosa pseudoharengus*, and the gizzard shad, *Dorosoma cepedianum*, in the Great Lakes. Transactions of the American Fisheries Society 86:97–111.

Morsell, J. W., and C. R. Norden. 1968. Food habits of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. Proceedings of the Conference on Great Lakes Research 11:96–102.

Muzzall, P. M. 1989. Endohelminths of salmonids from two localities in Lake Michigan, with emphasis on *Echinorhynchus salmonis*. Canadian Journal of Zoology 67:1604–1607.

Rhodes, R. J., and T. S. McComish. 1975. Observations on the adult alewive's food habits (Pisces: Clupeidae: *Alosa pseudoharengus*) in Indiana's waters of Lake Michigan in 1970. Ohio Journal of Science 75:50–55.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Bulletin of the Fisheries Research Board of Canada No. 184.

Seng, R. L. T. 1975. Metazoan parasites of fishes of Cold Lake, Alberta: a community analysis. Ph.D. Thesis, University of Alberta, Edmonton. 170 pp.

Stromberg, P. C., and J. L. Crites. 1975. An analysis of the changes in the prevalence of *Camallanus oxycephalus* (Nematoda: Camallanidae) in western Lake Erie. Ohio Journal of Science 75:1–6.

Webb, D. A., and T. S. McComish. 1974. Food habits of adult alewives in Lake Michigan near Michigan City, Indiana, in 1971 and 1972. Proceedings of the Indiana Academy of Science 83:179–184.

Wisniewski, W. L. 1958. Characterization of the parasitofauna of an eutrophic lake (parasitofauna of the biocoenosis of Druzno Lake. Part I). Acta Parasitologica Polonica 6:1–64.